

**THE BIOLOGY AND ZOOGEOGRAPHY OF THE  
LEGUME-FEEDING PATAGONIAN-FUEGIAN  
WHITE BUTTERFLY *TATOCHILA THEODICE*  
(LEPIDOPTERA: PIERIDAE)**

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*Abstract.*—*Tatochila theodice* occurs in central Chile and (as three nominal subspecies) in Argentina from northwestern Patagonia to the Beagle Channel. It is unusual in its lineage in feeding on Leguminosae, including native species of *Vicia* and *Lathyrus* and probably introduced *Trifolium*. The early stages are so different from other known *Tatochila* that generic recognition may be warranted. The unusual distribution of the species can be understood in terms of glacial-interglacial vegetation dynamics in southern South America. The evolutionary basis for repeated switching from Cruciferous to Leguminous hosts in the Andean Pierini is not understood.

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This is the eighth in a series of papers describing the life histories of the Pierini of the Andean region. Because of its alleged Holarctic derivation, this is an important group for reconstructing the historical biogeography of the Andean biota (Brown, 1987; Descimon, 1986; Shapiro, 1989, 1990a).

The largest pierine genus of the Andean region is *Tatochila* Butler, which was monographed by Herrera and Field (1959). They identified five species-groups, based on male genitalic characters and wing patterns. Group A consists only of *T. theodice* Boisduval and its two subspecies, *gymnodice* Staudinger from southern Patagonia and northern Fuegia and *staudingeri* Field from southern Fuegia. The form of the aedeagus in Group A is unique in the Andean Pierini. The wing pattern is complete and invariant in both sexes; the ventral hindwing vein-lines are narrow and sharply defined. Although *T. t. theodice* occurs in metropolitan Santiago, Chile it has not been previously reared and its biology has remained a mystery. Unlike other Chilean *Tatochila*, it is restricted to riparian corridors in the Andean and Coast Range foothills, has no consistent association with normal pierine hosts, and will not oviposit on these plants in captivity (Kellner and Shapiro, 1983). Shapiro (unpubl. data) had by 1988 failed consistently to obtain ova from all three Argentine subspecies, using conventional pierine hosts. In Tierra del Fuego, *T. t. staudingeri* was found commonly where no such plants occur.

In the austral spring of 1988 detailed observations of this species were made from northwestern Patagonia to the Beagle Channel, leading to the rearing of both northern and far-southern populations and the discovery that Herrera and Field's Group A is even more differentiated from the rest of *Tatochila* than had been suspected. Detailed documentation of the geographic range of *T. theodice* also led to the recognition of a pattern of probable importance for the interpretation of regional biota in a Quaternary framework.

Adult *T. theodice* from the northern part of its range in Argentina (Loncopué, Neuquén at least to Esquel, Chubut) are indistinguishable from Chilean material. The type locality of *theodice* is uncertain. No type specimen has been found and no neotype designated, but Herrera and Field (1959, pp. 477–478) restricted the type locality to “central Chile,” apparently defined as from Los Andes (metropolitan Santiago) to Victoria, Malleco. The nominate subspecies thus occurs in two segments with almost no latitudinal overlap, separated by the high Andean crest.

The subspecies *gymnodice* was described from Punta Arenas, Magallanes, Chile; *staudingeri*, from Puerto Harberton in Argentine Tierra del Fuego. Herrera and Field had little material. Examination of over 100 Fuegian specimens reveals unambiguously that they intergrade completely. Although *gymnodice* is usual on the southern Patagonian mainland, I have not found any “pure” population of either subspecies in Fuegia. *Tatochila theodice* was the commonest butterfly near Río Grande, Argentine Tierra del Fuego in November 1988; both subspecies phenotypes and intermediates occur abundantly in a series of 56 ♂ 30 ♀ collected 25 November. In addition, the females are dimorphic (white and yellow), a previously unreported trait. Although this population cannot be characterized as one subspecies or the other, it is one of the southernmost known and offers a good comparison to the Chilean or northwestern Patagonian populations of nominate *theodice*. It will be referred to here simply as the “Fuegian population.”

#### MATERIALS AND METHODS

On 13 November 1988 a female was taken flying near watercress at Junín de los Andes, Neuquén, northwest Argentine Patagonia. The following day a large colony was found on a boggy hillside seep near the shore of Lake Nahuel Huapí at San Carlos de Bariloche, Río Negro. Many males were seen patrolling, and three females observed near but not in patches of watercress. When no ovipositions had been seen in two hours, one of these females was collected. It and the Junín female were confined with watercress and dandelion flowers, both kept fresh with Water-Piks. By 20 November both females had died and a total of 18 eggs and one first-instar larva was found. The eggs had been laid on watercress, dandelions and the sides of the container. This was the first oviposition secured from this species in 11 years of trying. As the eggs hatched it became evident that the larvae would (and did) starve to death rather than eat watercress. Recalling the unexpected legume-feeding habit of *Tatochila distincta* Joergensen (Shapiro, 1986) and the abundance of naturalized white clover (*Trifolium repens* L.) at both the Junín and Bariloche sites, I added this plant and the surviving larvae accepted it at once. These larvae form the basis for the descriptions of the early stages of nominate *T. theodice* below; they were reared on *T. repens* under uncontrolled conditions in transit, ultimately eclosing in Davis.

Observations were made at Río Grande, Tierra del Fuego from 24–27 November 1988. The vegetation of the Río Grande site is described in Shapiro (1990b). Two Crucifers were present: *Thlaspi magellanicum* Comm. ex Poiret and *Draba magellanica* Lam. Neither was common; their combined biomass could not possibly support so dense a butterfly population. Fortunately, it was realized almost immediately that the host plants were two species of herbaceous vetches (Leguminosae), *Vicia bijuga* Gillies and *V. magellanica* Hooker, which trail on the ground and within



clumps of bunchgrass. They form an enormous biomass which, however, is inconspicuous when they are not in flower. Numerous ovipositions by at least six different females were observed over three days. Eggs are laid singly on leaves and stems with little consistency in position. Captive females oviposited on both vetches as well as the larger native Fuegian vetch *Lathyrus magellanicus* Lam., which was not present at this site. Larvae initiated feeding at once on all three plants, but rearing in transit was again on the readily available *Trifolium repens*. (This plant is naturalized in pastures in Fuegia from which the native vegetation is largely extirpated and also occurs in towns. *T. theodice* does not occur in its habitats.)

Six wild-collected Fuegian females were confined singly for 3–6 days with dandelions and various combinations of other common native plants from the Río Grande site, none of which elicited any ovipositions. The plants used were: Cruciferae: *Thlaspi magellanicum*, *Draba magellanica*, *Cardamine glacialis* (Forster) D.C.; Primulaceae: *Primula magellanica* Lehm.; Oxalidaceae: *Oxalis enneaphylla* Cav.; Compositae: *Perezia pilifera* (D. Don.) Hooker & Arn., *P. magellanica* Lag., *P. recurvata* (Vahl.) Less., *Hypochaeris incana* (Hooker & Arn.) Hoffman & Dusén, and *Senecio magellanicus* Hooker & Arn. Failure of these females to lay under identical conditions to those eliciting abundant oviposition on legumes was treated as significant.

Over 50 Río Grande larvae were reared, and matings and a second lab generation (on *T. repens* in Davis) secured. During a brief stay in Buenos Aires a number of Legumes and non-Leguminous weeds were collected from urban vacant lots and offered to second- and early third-instar Río Grande larvae which had been eating *Trifolium repens*. Cuttings were presented in groups of 2–3 species, always including one Legume; larvae had been starved for at least 3 hr. The plants used were: Leguminosae: *Vicia benghalensis* L., *V. angustifolia* L., *Medicago lupulina* L., *Medicago hispida* Gaert., *Medicago arabica* (L.) Huds., *Melilotus alba* Desr. ex Lam.; Cruciferae: *Sisymbrium officinale* (L.) Scop., *Brassica campestris* L., *Lepidium bonariense* L.; Polygonaceae: *Polygonum aviculare* L.; and Chenopodiaceae: *Atriplex hastata* L. (= *A. patula* var. *hastata*). No feeding was observed after 12 hr and the larvae were returned to *T. repens*. Descriptions of the Fuegian population are based on notes from life and preserved material of the first generation from Río Grande.

## RESULTS

*Behavior and ecology: T. t. theodice.*—In northwestern Argentine Patagonia at the northern extreme of its range, the nominate subspecies is restricted to mesic habitats. It often occurs in creek bottoms fringed with willow, where it has a frequent (but misleading) association with introduced watercress, *Nasturtium officinale* R. Br. (Cruciferae). Males patrol along streamsides, often weaving in and out of willows. Both sexes visit flowers, particularly introduced dandelions (*Taraxacum officinale* L., Compositae). Both sexes may be found in *mallines* (wet meadows), but never on the intervening ridges in shrub-steppe. The distribution is thus discontinuous; since most *mallines* are used as pastures, most colonies occur on ranches. In the Lake District (Aluminé to Esquel) it becomes more generally distributed under more mesic climatic regimes, occurring in lawns and gardens in towns and along woods edges. Although there is a rich weedy and native Crucifer flora in this region, the only species whose ecological distribution resembles the butterfly's is watercress. *T. theodice* has never

been found associated with the native *Tropaeolum* (Tropaeolaceae), which are important pierine hosts.

*Fuegian population.*—At Río Grande this insect occurs in bunchgrass steppe. Adults fly in full sun only, with air temperature as low as 12°C and strong and turbulent winds. Activity was noted from about 1000 to 1745 hours. Both sexes thermoregulate in the same dorsal-basking attitude as *Parnassius* spp. (Papilionidae), with wings open flat at the sides and pulled down into a triangular configuration with the head at the apex. No other basking attitude was observed. Dandelion is visited frequently. Other flowers visited less often include the natives *Perezia* spp., *Primula magellanica*, and *Oxalis* spp.

Although *Hypsochila microdice* Blanchard was also abundant, virtually no inter-specific interaction was seen with this similar-sized white butterfly. Male *T. theodice* patrol in a seemingly haphazard manner over the grass tussocks, frequently dipping to avoid the wind or to court a female. Courtships are very brief; copulation occurs within 15 sec if at all (8 observations). Males are easily lured to ground by pinched female decoys. Male-male chases are frequent and brief (20 sec). The flight of this species is much less direct and strong than that of *H. microdice*. It is much more likely to be picked up and carried away by the wind, and much more evenly distributed over the steppe than *H. microdice*, which is clumped in areas with more bare soil and relief (Shapiro, 1990b).

*Life history: T. t. theodice.*—All color names in quotation marks, and color numbers, refer to Kornerup and Wanscher (1978).

*Egg* (Fig. 1). Erect, fusiform but relatively broad,  $0.88 \times 0.35$  mm. Chorion sculptured as illustrated, with about 13 vertical and numerous horizontal ribs; the vertical ribs forming a very distinctly beaded corona around the micropylar region. Light orange (6A6) when laid, turning slate gray  $\pm 10$  hr before hatching. Laid singly in captivity and afield. The larva eats a hole below the top of the egg at hatch, but consumes little if any more of the chorion. Time to hatch, 5 days.

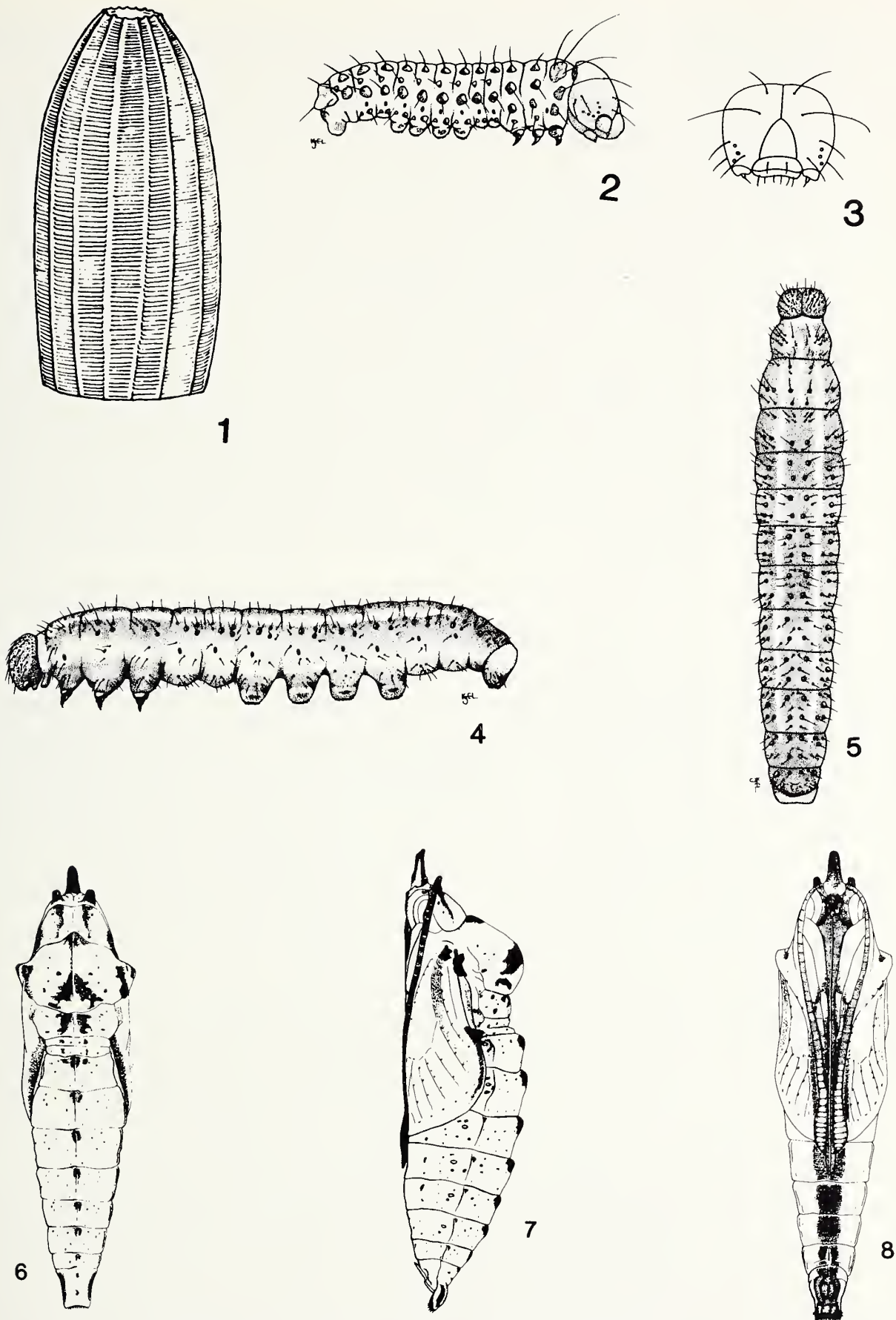
*Larva: First instar* (Figs. 2, 3). At hatch 0.97 mm. Light orange (6A6) with head apparently unmarked black; body darkening after feeding, becoming grayish. Tubercles in three sizes, black, bearing long primary setae. Feeds like a *Colias* larva, excavating strips between fine leaf veins, at rest on the midrib on the upper leaf surface between feeding bouts. Duration of instar, 2 days.

*Second instar.* After molt 1.9 mm long. Greenish gray (29D2), the usual *Tatochila* pattern of a dorsal median and subdorsal lines and a prothoracic collar, very pale yellow (5A5); tubercles black; head vaguely mottled dark brown and yellow. Habits as before. Duration of instar, 3 days.

*Third instar.* After molt 3 mm long. Slate gray ("greenish gray," 26C2), pattern as before, the dorsal line less distinct than the subdorsals. Head distinctly mottled with orange; ocelli and true legs black. Duration of instar, 5 days.

*Fourth instar.* After molt 7 mm long. Greenish gray (29D2); head black, mottled indistinctly with yellow ("absinthe yellow," 3C5), ocelli black; dorsal line faint, thin, whitish ("pale yellow," 3A3); subdorsal lines distinct, greenish yellow (3C5) tinged with orange ("dark orange," 5A8) to a variable degree, but especially on thorax and first two abdominal segments; a weak prothoracic collar, orange (5A8); area below the subdorsal lines gray (3D1) fading into dull yellow below the black spiracles, each segment containing an orange spot (sometimes two) within the yellow area; those on





Figs. 1–8. *Tatochila theodice theodice* from northwestern Patagonia. 1. Egg. 2. L<sub>1</sub> showing tubercles and setae. 3. L<sub>1</sub> head capsule. 4. L<sub>5</sub>, lateral view. 5. L<sub>5</sub>, dorsal view. 6. Pupa, dorsal view. 7. Pupa, lateral view. 8. Pupa, ventral view.

the thorax and first two abdominal segments usually strongest. Venter, including prolegs, dark slate gray (3E1); true legs black. Feeds openly on leaves, eating large holes. When disturbed, it drops from the plant. Duration of instar, 5 days.

*Fifth instar* (Figs. 4, 5). After molt 11.5 mm, reaching 29–31 mm. Pattern as before. Ground color dark ultramarine (20D7) with black tubercles bearing stiff black hairs, the tubercles smaller than usual for *Tatochila* but distributed as usual for the genus. Head pale bluish (23A3) mottled vaguely with orange and bearing black tubercles and ocelli. Mid-dorsal pale line bluish white, thin and not very distinct; subdorsal lines strong and contrasting, varying from bright orange-yellow (“orange,” 5A7) to pale yellow (5A6); spiracles black; subspiracular area very pale bluish white (22A3), each segment containing two brick red (9B8) spots, strongly contrasting; intersegmental membranes conspicuously yellow; venter and legs variable, as in fourth instar or distinctly purplish or greenish. In color this is the most variable *Tatochila* yet observed, and the yellow-to-orange subdorsal stripes produce quite different visual effects (orange makes the ground color appear more purplish than it is). In captivity the larva eats entire rosettes of clover, resting on the exposed rhizome or on the cage when not feeding; it drops if disturbed and is very active in general for a *Tatochila*. Time to prepupation, 10 days.

*Prepupa*. Usually vertical, head up, attached as usual by the anal prolegs and a silken girdle. Color initially as in last instar but losing contrast, becoming indistinct grayish but with the tubercles more prominent than previously; future wing-case areas distinctly olive green. Time to pupation, 30 hr.

*Pupa* (Figs. 6–8). Length 21 mm; width at girdle 5.4 mm. Attached by the cremaster and girdle as usual. Ground color light blue gray (“bluish white,” 23A2), tubercles black; dorsal midline with strong, black segmental keels; indistinct subdorsal lines, creamy white; top of head and eyes cream; legs, antennae and proboscis cases always chocolate brown (10F5); chocolate brown pattern otherwise extremely variable, from nearly absent to nearly covering the dorsum. Three prominences on head, mostly chocolate brown, the frontal prominence more than twice the length and width of the others and slightly curved dorsad. This is the strongest frontal prominence yet seen in *Tatochila*; it is reminiscent of the pupa of *Ascia*.

Eyes, wings and body pigmented in that order, white first appearing 40 hr and the black pattern roughly 24 hr before eclosion. Meconium bright red, as in other Andean Pierini (Shapiro, 1982). Time to eclosion (non-diapause), 17–20 days.

*Fuegian population*.—The life history of the Río Grande population is similar to that of northern *T. t. theodice*. All stages are smaller, but grow faster at the same temperatures. The following phenotypic differences were noted:

*Egg*. When laid, reddish orange (7A7) (slightly darker than *T. t. theodice*).

*Larva: Fifth instar*. Length at maturity 23 mm. Ground color dark bluish to violet gray (“dull violet,” 18D4), the dorsal line white. Subdorsal lines broader than in nominate *theodice*, orange-yellow (4A8), as in the collar. Spiracles black; subspiracular area ice-gray (15B1), scarcely if at all yellowish, darker ventrad, with the usual orange spots; head mottled, bluish gray (20B3) and pale orange (“peach,” 7A4), ocelli black; venter greenish gray (27B2), prolegs distinctly purplish (“lilac,” 15B4); true legs black. Color more constant than in the nominate subspecies, but if anything even less typical for the genus.

*Prepupa*. As in *T. t. theodice*, but livid purple (“grayish magenta,” 13B4)—exactly



the color of the prepupa of the North American Pierid *Euchloe hyantis* W. H. Edwards. This color change has not been seen previously in the Andean fauna.

*Pupa.* Smaller than *T. t. theodice* (18 × 4.5 mm), similar in form but the frontal prominence slightly less developed. Ground color initially purple (13B4) but turning fawn-buff (5A3) in about 40 min. Chocolate brown pattern highly variable as in the nominate subspecies. Facultative pupal diapause was observed, but the factors controlling it were not investigated. This population is bi-, perhaps partially trivoltine. Time to hatch (non-diapause), 13–17 days. Diapause pupae require at least 3 months of refrigeration at 2°C. In the lab-reared second generation, at L:D 14:10 hr, day/night temperatures 21°/10°C, the average development time, egg to adult, was 41 days.

*Hybridization experiment.* A reared Río Grande male was mated with a reared Junín-Bariloche female. Only 10 eggs were laid although the female lived for nearly a month; males were nearly constantly present but she never remated. Five of the eggs hatched and one larva pupated, but died without eclosing. Both the larva and pupa were larger even than nominate *theodice*. Since no difficulties were observed in rearing pure second-generation Río Grande animals eating the same food in the same growth chamber, genetic incompatibilities are suspected.

#### DISCUSSION

*Taxonomic status.*—Throughout its life history, *Tatochila theodice* displays apparently uniquely-derived attributes similar to those distinguishing genera in the Pieridae. The aedeagal morphology, used by Herrera and Field to distinguish their Group A, could indeed define a genus on its own, but these authors were quite conservative. Among traits which differentiate *theodice* from other *Tatochila* whose life histories are known are: the strong corona of the egg, apparently obligate use of Leguminous hosts, reduction of the larval tubercles, larval color scheme, very strong frontal prominence in the pupa, and drop-and-curl defensive behavior of the larva. However, I am refraining from naming a new genus to contain *T. theodice* until all of the “species-groups” of *Tatochila* have been reared and a phylogenetic analysis incorporating developmental characters has been completed.

The subspecific differences in the late larva, prepupa and pupa all suggest that Fuegian populations are derivative. The prepupal–early pupal color is an autapomorphy relative to the entire Andean Pierid fauna. The polarity of these morphoclines is of interest in interpreting the biogeographic history of *T. theodice*.

*Quaternary migrations and contemporary distributions.*—The distribution of this butterfly at first appears very strange. Although most of the historic references to it are Chilean, its distribution there is limited to a narrow latitudinal band (32°51' to 38°15'S) around the edges of the Central Valley in a Mediterranean climate. Within this range there is no geographic variation in adult phenotype. In Argentina, where all the subspecies occur, its northernmost population is at Loncopué, Neuquén (38°04'S). There is thus hardly any latitudinal overlap, though it is possible that undetected populations exist especially on the Chilean side. Between the ranges, inhospitable Andean habitats intervene with elevations consistently over 2,000 m. The distribution of the species extends thence southward in the eastern foothills of the Andes all the way to Tierra del Fuego. *T. theodice* is absent from all of southern

(including archipelagic) Chile in these same latitudes, re-entering Chilean territory only in the steppe near Punta Arenas, and then from the east.

Caviedes (1990) has provided a paleoclimatic model consonant with the historical-biogeographic scenario advanced by Heusser (1981, 1983) and Caviedes and Iriarte (1989) for the evolution of the temperate biota of the Southern Cone in the Quaternary. This model fits the known distribution of *T. theodice* extremely well and renders it comprehensible. The present distribution of *T. theodice* strongly implies that it is intolerant of the very wet conditions prevailing today in austral latitudes west of the Andean crest. It is typical in Quaternary biogeographic reconstructions to assume little if any change in the climatic tolerances of species, i.e., climates change faster than adaptations do; otherwise it would be impossible to limit the number of hypotheses in the absence of fossil evidence.

In Caviedes' model, during Pleistocene glacial maxima pluvial conditions extended much farther north, and the high passes of the Cuyo district (Mendoza, San Juan), which are today unforested and summer-xeric, would have been forested, mesic, and potentially suitable for trans-Andean dispersal of *T. theodice* into its present Chilean range. Subsequently, mesic vegetation retreated drastically on both sides of the Andes and the Monte desert developed east of the crest, driving *T. theodice* south of the Cuyo into Neuquén. The passes in Neuquén, Río Negro and Chubut which are mesic today (and permeable to *theodice* northward but not in the south, where the Chilean side is too wet) were icebound in full-glacial time, and the lower Chilean altitudes somewhat wetter even than today. The confinement of *T. theodice* to the limited mesic ecotone between *Nothofagus* forest and the Patagonian steppe again suggests it would have been unable to occupy full-glacial southern Patagonia or Fuegia, whose climates were much harsher. Thus, both the entire Chilean range and the austral Argentine distribution of this butterfly are probably of Quaternary origin—the former full-glacial, the latter post-glacial.

*The use of legumes.*—The native host of *Tatochila theodice* in its northern range remains undetermined. There are several native Legumes in the region whose ecological and geographic distributions fit the butterfly's well; they include (in Chile) *Vicia vicina* Clos., *Lathyrus hookeri* D. Don., and *Astragalus berterianus* Reiche. In northern Patagonia the distribution of the butterfly closely parallels that of naturalized clover in *mallines*, but actual use in the field remains to be documented and no native candidate hosts have been identified. (The native Andean *Colias* are nearly all recorded only on introduced clovers and alfalfa, though ancestral use of *Lupinus* and *Astragalus* seems likely. Many of the Crucifer-feeding Pierini likewise are known only from naturalized European weeds (Kellner and Shapiro, 1983).)

The principal host associations of Pierini globally are Loranthaceae and the set of mustard-oil-producing families (Cruciferae, Capparidaceae, Resedaceae and the more distantly-related Tropaeolaceae) (Ehrlich and Raven, 1964). Cruciferae and Tropaeolaceae are widely distributed in the Andes. The former may have entered as recently as the Great American Interchange (3 MYA), but the latter are autochthonous. Legumes are ancient, ancestral hosts of two other Pierid groups, the Coliadinae and Dismorphiinae, but except for the genus *Colias* and the Palearctic *Leptidea*, these animals feed not on Papilionaceae but on Mimosoid and Caesalpinoid Legumes. The scattershot occurrence of Legume-feeding in *Tatochila* and *Hypsochila* (Shapiro, 1986, 1990a, b) suggests it is a derivative condition which has arisen several times



in the Andean Pierini. All the native hosts (*Astragalus*, *Vicia*, *Lathyrus*) are, moreover, advanced Papilionaceae which probably entered South America in the Great American Interchange (Raven and Axelrod, 1974). *Colias* is probably also only of Quaternary vintage in the Andes (Descimon, 1986; Shapiro, 1990a). *Tatochila* and its relatives have traditionally been considered Quaternary derivatives from the Holarctic as well (Dixey, 1894; Elwes, 1894; Grote, 1900), but this scenario is increasingly untenable (Shapiro, 1990a).

“Convergent or parallel evolutionary change repeated across diverse taxa and accompanied by evidence of similarity of selective forces is unlikely to occur by chance alone” (Pagel and Harvey, 1988). Are there obvious ecological “selective forces” favoring a repeated shift from mustard oil plants to Papilionaceous Legumes in the Andean-Patagonian fauna? In Fuegia, the biomass of native Legumes in *Tatochila-Hypsochila* habitats far exceeds that of Crucifers and allows the maintenance of very dense populations and the occupation of communities otherwise closed to Pierini. However, in the case of *Tatochila theodice*, as noted above, occupation of the far south is probably a recent development, while Legume-feeding must have evolved farther north.

Cases of parallel host-switching suggest the existence of chemical “bridges” among the plant taxa (Ehrlich and Raven, 1964; Ehrlich and Murphy, 1988). If there are such bridges between the Cruciferae and the Papilionaceous Legumes, it is odd that they have not been crossed in the Northern Hemisphere, where appropriate Pierini and all the plant genera concerned are well represented. On the other hand, the apparent unacceptability of the various Legumes, including *Vicia* spp., from Buenos Aires to *Tatochila theodice* suggests that the far-southern vetches may be chemically “special.” The one obvious chemical trait they display is indigo production (Shapiro, unpubl.), but this is not a Crucifer trait. The basis for Legume-feeding by *Tatochila* is a mystery.

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